Comb Architecture of the Eusocial Bees Arises from Simple Rules Used During Cell Building

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Abstract

The brood cells of a colony of eusocial bees are a core part of its existence. Not only do the cells provide a nursery for the brood, but they also provide the structure on which the colony lives. As such, the comb structure is itself under natural selection to provide an environment in which a colony can thrive. Via examples from the stingless bees and the honey bees, we show that aspects of nest construction arise from simple rules followed by workers as they build cells and that these rules are species specific. Slight changes in the rules followed by cell builders can cause radical shifts in the final nest architecture, and these are often used by humans as species diagnostic traits.

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1. INTRODUCTION

There are four tribes of corbiculate bees (Hymenoptera, Apidae): the orchid bees, Euglossini; the bumble bees, Bombini; the stingless bees, Meliponini; and the honey bees, Apini. The diversity of nest architecture within the group is remarkable. Nests vary from the single brood cells constructed by the solitary orchid bees to the massive nests containing tens of thousands of specialized cells constructed by some stingless bees and honey bees.

All corbiculate bees construct nests based on a fundamental building block, the cell (Michener, 1964). All cell types are presumably derived from an ancestral cell type similar to those constructed by extant solitary bees. The primitive brood cells of solitary bees are based on a chamber, usually excavated in soil or plant material by a female, and often lined in some way. The female furnishes her brood cell with pollen, upon which her offspring will feed. The mother lays an egg on the pollen mass, seals up the cell, and moves on to the next construction project. The cell provides the developing offspring with some protection from desiccation, predation, parasitism, and infection. This is apparently a winning combination, because brood cells have been retained in all eusocial bees, despite the expense of construction. This contrasts with the ants, in which brood are reared in piles inside the nest (Hölldobler and Wilson, 1990).

The next stage in the evolution of bee nests was the development of aggregations of brood cells similar to those seen in the Halictidae (Michener, 1974). Such aggregations may or may not have comprised related individuals or the offspring of a single female. They probably evolved in response to a limited availability of nesting sites, obliging the bees to create brood cells in close proximity to others. When brood cells are highly aggregated, there is the possibility that the aggregation will gain some emergent structure, and natural selection can act to engender behaviour that enhances the survival of the group of cells. This might include cooperative defence of the nest or the construction of a drainage tunnel or ventilation shafts that improve the environment within the brood chamber as seen in the Halictidae (Michener and Lange, 1958).

When brood cells are built so that they touch each other, structure can emerge from the arrangement of the cells themselves. There may be an optimal distance between individual cells, which facilitates access by adults to the developing brood, or that enhances gas exchange, or the retention, or dissipation of heat. The arrangement of brood cells in the nests of bumble bees

probably reflects selective pressures of this kind. The cluster of brood cells is spherical, and honey pots are on the periphery of the nest. This arrangement no doubt facilitates the thermoregulation of the nest.

The most 'recent' stages of nest evolution are seen in the stingless bees and the honey bees. Here, the cells are constructed contiguously and form a comb, which we define as a collection of cells constructed without gaps between them, or a semi-comb, where there are gaps between some of the cells, or a cluster where cells do not touch and are joined by pillars. Combs have many advantages over clusters including minimizing the use of materials, sharing of metabolic heat by the developing brood, and strength. A nest based on comb can be self-supporting and constructed in the open, removing the need for cavities, which can be a limiting resource (Koeniger, 1976). Yet the arrangement of cells into combs comes at a cost, for the cells within combs need to be recycled in some way. In the honey bees, brood cells are used repeatedly, increasing the risk of intergenerational disease transmission. In the stingless bees, the comb has to be rebuilt with every generation of brood that emerges, meaning that the comb is a dynamic structure that changes over time as it is continuously destroyed and rebuilt (Michener, 1961).

In this review, we discuss how comb structure emerges during the cell building process in stingless bees and honey bees. Each species has a unique nest architecture, and there can be radical differences between species that are nonetheless phylogenetically similar. Indeed, nest architecture alone is often used as a species-defining character, especially in the stingless bees (Franck et al., 2004), and to distinguish the two dwarf honey bees (Oldroyd and Wongsiri, 2006; Rinderer et al., 1996).

2. BUILDING FROM A BLUEPRINT OR STIGMERGY?

In contemplating a eusocial bee's nest, it is tempting to conclude that its construction is guided by an innate blueprint possessed by each of its builders (Thorpe, 1963). It is more likely, however, that bees resemble other insect architects in lacking an explicit image of the nest's final design. Mud wasps (Smith, 1978) and termites (Turner, 2010), for example, can be induced to build structures that radically depart from normal nests through targeted interference at critical stages of construction. If the insects possessed a blueprint, we would expect them to use it to regulate their nest to the intended pattern.

Comb building may be better explained by the competing hypothesis of stigmergy, which holds that appropriate building behaviour is stimulated by previous construction (Camazine et al., 2001; Grassé, 1959). That is, each builder works according to an algorithm that tells her what to do when she encounters a structure at a particular stage of development. Her actions advance the structure to a new form that in turn stimulates the appropriate next step, either by her or by the next worker to encounter the building site. The canonical example is arch construction by termites, which is thought to be initiated by random placement of mud pellets (Grassé, 1959). Once deposited, a pellet becomes more attractive as a deposition site for subsequent pellets, concentrating the termites' activity so that they gradually build a pillar of mud. Once this pillar reaches a certain height, it in turn stimulates addition of sideways extensions that link with neighbouring pillars formed by the same mechanism.

Direct evidence for stigmergic comb construction by bees is lacking, but it appears to play a role in paper wasps' building of their comb-like hexagonal cell arrays. For example, construction begins with a petiole that extends downwards from a horizontal substrate. A short petiole induces builders to extend it, but once it reaches a critical length, the petiole instead stimulates construction of a flat sheet that eventually forms a wall of the first cell (Downing and Jeanne, 1988). Modelling studies inspired by wasp nests further show that structures that are amazingly similar to real wasp nests can emerge from stigmergic behaviour (e.g. Theraulaz and Bonabeau, 1995). A conceptual advantage of these models is that they account for the highly distributed nature of building behaviour. Close observation of honey bees shows that each cell emerges from small contributions by many workers rapidly coming and going at the building site (Hepburn et al., 2014). Stigmergy allows any worker to pick up where the last one left off, as long as every worker follows the same rules.

The rules that account for a particular species' distinctive nest are heritable and more or less constant for that species. Their modification across species can account for the remarkable taxonomic diversity of nest designs. Even slight changes in cell construction rules can lead to the development of radically different structures. For example, when several cells are constructed simultaneously and back to back, they will form a comb structure as seen in the honey bee comb. If the rule is to build a pillar between cells, the emergent structure will be a semi comb as seen in the stingless bee, *Tetragonula hockingsi* (Fig. 1; Brito et al., 2012).

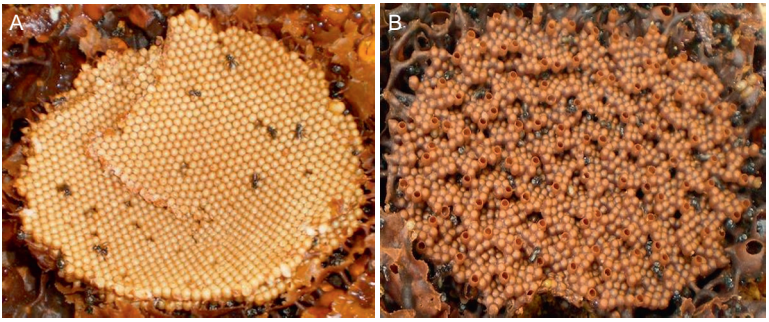

Figure 1 Contrasting nest structure of two closely related Australian stingless bees. (A) The spiral of *Tetragonula carbonaria*. (B) The semi-comb brood comb of *T. hockingsi*. The alternate brood structures can emerge by a small change in the rules of how cells are joined. *Photos by R. Brito.*

Within a species, rules may be context-dependent, varying adaptively according to colony age, size, nutritional status, or reproductive state. For example, a honey bee worker builds different kinds of cells for different purposes and must apply different rules so that cells of the right kind are built at the right time in the right place. In the dwarf honey bee, *Apis florea*, the larger drone cells are constructed on the lower margin of the single comb (Fig. 2). But drone cells are seen in the largest nests and quite small ones, meaning that drone cells must be removed and replaced with the smaller worker cells as the comb grows. How the workers 'know' which rule to apply is mostly unknown.

3. ON THE FORMATION OF HEXAGONAL CELLS

How bees produce such a remarkably regular array of hexagonal cells has challenged biologists for centuries (Darwin, 1859; Hepburn et al., 2014; Huber, 1792; Lau, 1959). The two-sided combs of honey bees impressed nineteenth-century mathematicians with their answer to a difficult problem in geometry: how to maximize volume for minimum surface area in an array of close-packed cylinders (Ball, 1999). The bees' two-layered array of hexagonal cells joined by triple-rhomboid bases (Fig. 3) gives an apparently optimal solution (Taylor, 1976; Thompson, 1917; Tóth, 1964). Applying the logic of natural selection, Darwin (1859) argued that this form arose over evolutionary time through gradual modification of a set of building rules, with selection favouring increasingly efficient usage of wax.

Figure 2 The comb of a large *Apis florea* colony offered for sale by a honey hunter on a street corner in Bangkok. The larger cells at the bottom of the comb have been constructed for the rearing of drones. The smaller cells are for the rearing of workers and the honey store is at the top. Circles of sealed cells in the worker comb arise from the history of the comb's construction. As the colony expands, new worker comb is added at the margin of the comb, and drone comb at the bottom. The drone cells must be removed by cell-constructing workers before new worker cells can be constructed. *Photo by B. Oldroyd.*

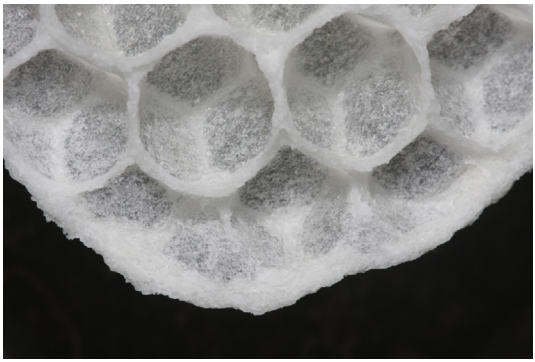

Figure 3 Cells under construction by *Apis mellifera*, showing the highly regular array of hexagonal cells with rhomboid bases. *Photo by B. Oldroyd.*

In a reaction to Darwin's adaptationist paradigm, Thompson (1917) argued that the optimal solution could instead result from physical necessity combined with very rudimentary behaviour. He wrote: 'the direct efforts of the wasp or bee may be supposed to be limited to the making of a tubular cell, as thin as the nature of the material permits, and packing these little cells as close as possible together. It is then easily conceivable that the symmetrical tensions of the adjacent films … should suffice to bring the precise configuration which the comb actually presents.' The laws of thermodynamics would cause the wax to achieve the optimal, energy-minimizing configuration, with no need for complex building behaviour finely honed by natural selection.

Thompson's hypothesis is appealingly simple, but it does not seem consistent with currently available data on actual bees. Pirk et al. (2004) reported that molten beeswax poured around an array of beads could form a regular lattice of cavities, but they did not show that bees deploy their bodies in an analogous way nor, more importantly, that natural building sites are sufficiently warm to yield flowing wax. Later observations of building bees using thermographic video have shown that the comb temperature is consistent with solid, not liquid wax (Bauer and Bienefeld, 2013). Karihaloo et al. (2013) offered a more detailed model for a Thompson-like scenario based on measured physical properties of beeswax. The model shows how initially round cells may quickly adopt a hexagonal form as a result of the flow of visco-elastic molten wax near the triple junction of neighbouring cells. However, this model also assumes heating to temperatures not known to occur in actual comb.

Detailed observation of building bees makes clear that they actively bite, form, and plane the developing cells, rather than forming a passive matrix around which wax flows (Bauer and Bienefeld, 2013; Hepburn et al., 2007; Martin and Lindauer, 1966). Further, hexagonal cells are also typical of social wasps like *Polistes* and *Vespula*. These cells are constructed from macerated plant material, a substance much less likely to have the thermoplastic properties of warm wax (Downing and Jeanne, 1988, 1990). These facts suggest that comb construction depends on context-dependent rules that the bees (and wasps) follow depending on the kind of cells required (Downing and Jeanne, 1990). Thus, it seems unlikely that a simple emergent process based on the fluid properties of molten wax can explain the remarkable orderliness of the bees' comb. Nonetheless, the physical properties of wax doubtless interact with the building rules of the bees, and a solution to the puzzle of comb construction will have to account for both components.

It is important to note that combs of social bees and wasps are almost certainly independently derived, since the common ancestor of the bees, wasps, and ants (Misof et al., 2014) was no doubt solitary and therefore did not construct comb. Thus, both bees and wasps have converged on the hexagonal cell shape, presumably because this shape provides the most strength for the least material (see references above).

4. THE HONEY BEES

There are three groups of honey bees (*Apis*) that are sometimes regarded as subgenera: the dwarf bees (*A. florea* and *A. andreniformis*), the giant bees (e.g. *A. dorsata* and *A. laboriosa*), and the cavity-nesting bees (e.g. *A. mellifera* and *A. cerana*; Fig. 4). The dwarf bees are thought to be the most basal (Lo et al., 2010; Ruttner, 1988). They build a single comb *around* a twig. The 'crown' of the nest is built above the twig. The crown serves as the honey-storage area, and as a platform for communication dancing by foragers (Dyer, 1985; Oldroyd and Wongsiri, 2006; Rinderer et al., 1992). The crown is integral to the structural integrity of the nest and supports the protective curtain of worker bees that shields the nest from the elements (Dyer and Seeley, 1991).

The nest of the giant bees differs from the dwarf bees in that the single massive comb is built *beneath* a support, which may be a cliff overhang, the

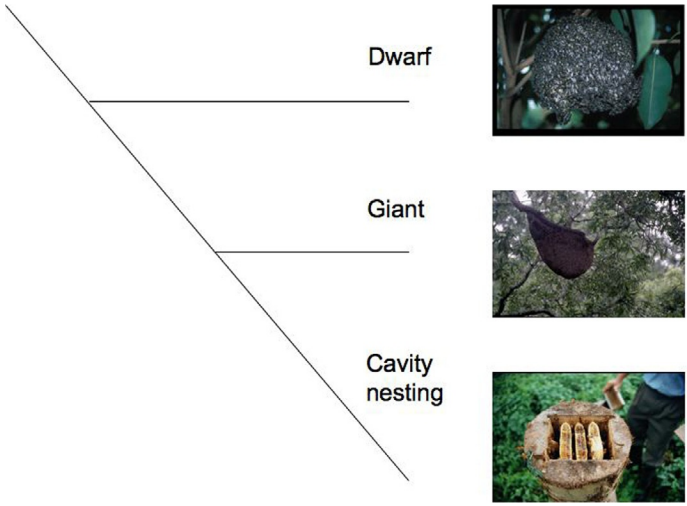

Figure 4 Phylogenetic relationships and comb structures of the honey bees *Apis*. *Photos by B. Oldroyd.*

eve of a building, or a sloping branch (Oldroyd and Wongsiri, 2006). Relative to the comb of the dwarf bees, the comb of the giant bees has multiple design flaws. Because the comb lacks a crown, it is much less well anchored to the support than a dwarf bee comb is, and it is not uncommon to see the comb of a giant bee colony broken off its support during a storm, or knocked off by an attack from predatory birds (Thapa and Wongsiri, 2003). When constructed under a branch (rather than in a rock shelter), the nest is vulnerable to inundation, for the protective curtain of workers is broken at the site of attachment of the comb to the branch. The poor design of giant bee combs suggests that the ancestral species (like extant *A. laboriosa*) always nested under cliff overhangs where the crown structure could not be built, and the cliff afforded protection from rain and wind. Although *A. dorsata* often nests on the limbs of trees, it has yet to (re)evolve the crown that is seen in the dwarf bees. The cavity-nesting bees build parallel combs within a cavity. Their nests benefit from the protection afforded by the cavity, but this clade of bees pays the price of much reduced nest site availability, and limits to colony growth (Inoue et al., 1990).

5. DWARF HONEY BEES

5.1 A Species Difference in Comb Morphology

There are two species of dwarf bee. They are phylogenetically similar (colonies of one species accept a queen of the other) and may have diverged as recently as 10,000 years ago (Oldroyd and Wongsiri, 2006). The comb architecture of the two species is almost identical, but with one fundamental species-specific difference (Fig. 5): the construction of the crown. In *A. andreniformis*, the crown is constructed with a midrib that protrudes vertically from the upper margin of the supporting twig. In *A. florea*, all cells of the crown are joined directly to the branch (Figs. 5 and 6; Rinderer et al., 1996). This arrangement requires that the cells of the crown of an *A. florea* nest be fluted at as it extends outwards from the supporting twig (Fig. 6).

While to our knowledge this matter has never been specifically investigated, it is clear that the species-specific architecture arises as an epiphenomenon of the way the first cells of the crown are constructed. In *A. andreniformis*, the cells are constructed on the horizontal and in the same line as the cells below the supporting twig. In *A. florea*, they are built outwards from the twig, as if the twig itself acts as a *de facto* midrib (Fig. 7).

Figure 5 The differing structure of the crown of the nest in the dwarf honey bees. Top, *Apis florea*; bottom, *Apis andreniformis. Photo by B. Oldroyd.*

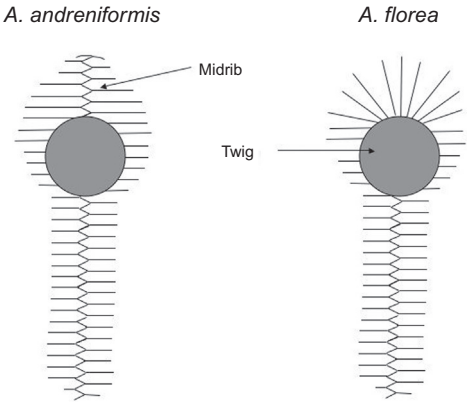

Figure 6 Cross section of the combs of *Apis florea* and *Apis andreniformis* showing the different crown structure.

5.2 *A. florea* Can Build Under a Flat Surface

Occasionally, *A. florea* nests are seen which are built on a horizontal or vertical surface. In these unusual nests, the crown is attached directly to a vertical surface. This means that the rules that normally result in the construction of the crown of the nest can be modified if the founding swarm somehow finds itself on a vertical surface.

5.3 Different Rules Depending on the Queen State

In *A. florea*, a common response to the loss of their queen and the means to raise another one is for the workers to abandon their nest and form an

Figure 7 A nest of *Apis florea* in which the honey-storage crown has been scraped off by a honey hunter. The direct attachment of the base of the cells to the supporting twig is clearly evident. *Photo by B. Oldroyd.*

orphaned colony. The likely functional significance of 'absconding' behaviour is to reduce rates of reproductive parasitism by workers from other nests and to allow the colony to build a comb suitable for the rearing of males rather than workers (Chapman et al., 2010). The workers, being unmated, can only produce male-producing eggs. Drones reared in smaller worker cells are diminutive, and so it is far better to raise drones in drone-sized cells. The brood combs of orphaned nests are comprised entirely of drone-sized cells (Fig. 8), meaning that the queenless workers change the rules of cell construction in response to their queen state. They may even retrieve wax from their abandoned comb and refashion it into drone comb, for workers are often seen retrieving wax from abandoned combs (Fig. 9).

The ability to adaptively change a rule (construct drone-sized cells instead of worker-sized cells) means that workers perceive their queen state and adaptively change the architecture of their nest to rear males.

6. GIANT HONEY BEES

The giant bees have the simplest nest architecture of all the honey bees. Unlike the other species, all cells of the giant bee comb are of identical diameter (Tan, 2007). They only vary in their depth, with cells destined to store honey greatly elongated (Tan, 2007). Honey-storage cells are always attached directly to the support on the higher side of the colony

Figure 8 Comb built by a queenless *Apis florea* colony. Most cells are for rearing drones and there are no worker-sized cells. *Photo by N. Chapman.*

Figure 9 *Apis florea* workers retrieving wax from an abandoned comb. *Photo by B. Oldroyd.*

Figure 10 In *Apis dorsata*, the cell diameter is uniform across the entire nest. The honey-storage cells (top right) are the same diameter as the brood-rearing cells but are greatly elongated. *Photo by B. Oldroyd.*

(Fig. 10). The reason why the giant bees need only one cell size is probably because the workers have not undergone the reduction in size seen in the other species: drones and workers are of similar size. Nonetheless, like all honey bee species, the males are reared on the margin of the comb in freshly produced cells (Chinh et al., 2004). This is interesting, because there seems no intrinsic reason why drones (and drone cells) should be on the comb margins. Perhaps, the males are less sensitive to temperature fluctuations during their development, or the reduction in cognitive abilities that seems to arise from suboptimal rearing temperatures is less important in males than it is in workers (Jones et al., 2005).

7. CAVITY-NESTING HONEY BEES

The transition to nesting in cavities constricts the horizontal length of a comb, sometimes quite severely. This may have forced the transition of a defining feature of nest architecture of the cavity-nesting bees, the parallel combs. Belic et al. (1986) showed that parallel combs can emerge as a self-organized process.

8. STINGLESS BEES

8.1 General Plan of a Stingless Bee Nest

Stingless bees (Meliponinae) reproduce similarly to solitary bees: an egg is laid on top of a food mass in a single cell, which is then sealed (Roubik, 2006; Sakagami, 1982). Stingless bees have an amazing variety of nest types (Rasmussen and Camargo, 2008; Wille and Michener, 1973). Typically, but not always, stingless bee colonies nest in a cavity. The brood area comprises a dense aggregation of brood cells that is usually surrounded by a covering of multilayered wax and resin called the involucrum, the purpose of which is to protect the brood nest and insulate it (Fig. 11). Outside the involucrum, there is an area of large waxen storage pots where the bees store pollen and honey. The nest is often sealed off from the rest of the cavity by one or more plates of resin called the batumen plates. The nest can be connected to the outside via a waxen entrance tube, which may extend into the air for many centimetres (Fig. 12).

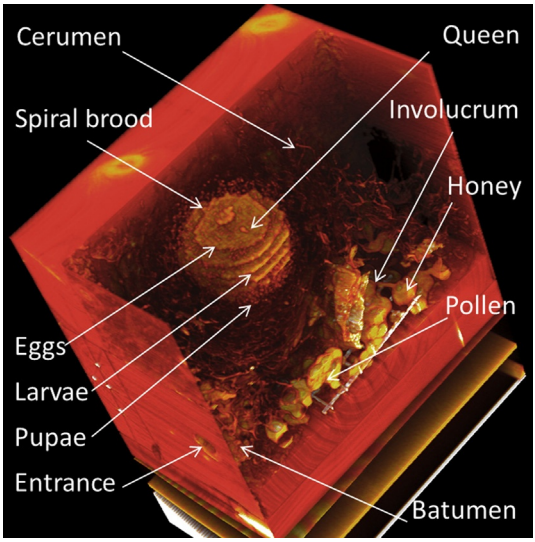

Figure 11 The internal architecture of a typical stingless bee nest (*Tetragonula carbonaria*). The spiral brood comb is in the centre, surrounded by storage cells, connecting involucrum, and insulating batumen. *X-ray image courtesy of Dr. M. Greco.*

Figure 12 The entrance tube of a *Trigona collina* colony. *Photo by B. Oldroyd.*

8.2 Combs and Clusters

Unlike the honey bees, the cells of the Meliponini do not have common walls, and the cells can be separated. To human eyes, one of the key species-specific traits is whether the brood cells are constructed as a comb, semi-comb, or a cluster.

An interesting example of the comb/semi-comb dichotomy is provided by the *Tetragonula* species complex from the east coast of Australia. This group comprises four species (Table 1). Workers of all species are extremely similar morphologically and show latitudinal clines in size. The similarity of worker morphology combined with the clines makes identification of species based on worker morphology difficult or impossible (Dollin et al., 1997). Nonetheless, taxonomists were convinced that the group comprised multiple species because of differences in nest architecture. The arrangement of the brood cells, and the morphology of the nest entrances, varies strongly across the group. *Tetragonula carbonaria sensu stricto* builds a spiral brood comb, whereas its sibling species *T. hockingsi* builds a semi-comb (Fig. 7; Michener, 1961). As *T. carbonaria* has a range that extends well into the temperate zone, and as far south as Sydney, and *T. hockingsi* is restricted to the north, we were suspicious that the difference in nest architecture was an example of phenotypic plasticity in response to temperature, and in fact the two taxa were a single species. Thus, we postulated that the northern *T. hockingsi* was merely a comb phenotype built in tropical regions, whereas the *T. carbonaria* comb type was a more heat-conserving form built in temperate climates. This turns out to be incorrect.

Table 1 Evidence for a Likely Association Between Synchronous or Asynchronous Cell Construction on the Overall Nest Architecture of Stingless Bees

Cell Construction	Type of Comb	Species	References
Successive	Cluster	*Austroplebia symei*	Drumond et al. (1999)
Successive	Cluster	*Austroplebia australis*	Drumond et al. (1999)
Successive	Cluster	*Plebeia minima 2*	Drumond et al. (1999)
Successive	Cluster	*Trigona laeviceps*	Sakagami et al. (1983)
Successive	Cluster	*Trigona pagdini*	Sakagami et al. (1983)
Successive	Cluster	*Trigona clypearis*	Dollin et al. (1997)
Successive	Cluster	*Tetragonula sapiens*	Dollin et al. (1997)
Synchronous	Semi-comb	*Tetragonula hockingsi*	Dollin et al. (1997)
Synchronous	Cluster	*Tetragonula mellipes*	Dollin et al. (1997)
Synchronous	Comb	*Plebeia saiqui*	Drumond et al. (2000)
Synchronous	Comb	*Plebeia nigriceps*	Drumond et al. (2000)
Synchronous	Comb	*Plebeia wittmanni*	Drumond et al. (2000)
Synchronous	Comb	*Plebeia minima 1*	Drumond et al. (2000)
Successive	Comb or spiral	*Plebeia poecilochroa*	Drumond et al. (1995)
Synchronous	Spiral comb	*Tetragonula carbonaria*	Dollin et al. (1997) and Yamane et al. (1995)

The numerals in the *P. minima* species names refer to putative subspecies.

We have made extensive collections of stingless bees along the east coast of Australia. Molecular phylogenetic analysis of these collections has revealed at least four species and confirmed that the morphology of the brood nest is indeed different between the species (Brito et al., 2014; Franck et al., 2004). A new species that builds the semi-comb nest structure was identified near Brisbane. Molecular genetic evidence shows that this species, *T. davenporti*, shows strong divergence from all other Australian species

and groups with Asian species of the *T. laeviceps* group (Franck et al., 2004). *T. mellipes* seems to be restricted to tropical north Queensland. Interestingly, *T. hockingsi* seems to be replacing *T. carbonaria* in the suburbs of Brisbane, a fact that has been attributed to increasing temperatures (T. Heard, personal communication).

Another species-specific trait of the *T. cabonaria* group is the ornamentation of the entrance hole (Table 1). *T. carbonaria sensu stricto* surrounds their entrance hole with a 4-cm wide layer of resin. *T. melipes* builds an entrance tube that extends out several centimetres. *T. davenporti* and *T. hockingsi* have virtually no ornamentation at all. The differences in entrance ornamentation may be highly significant to the integrity of species. Drones fly in mating swarms in front of colonies and may use the morphology of the entrance to identify conspecific nests. This may not be entirely successful, because we believe that we have identified a few *T. hockingsi*/*T. carbonaria* hybrids (Brito et al., 2014).

8.3 Combs, Semi-Combs, Clusters, and Spirals

It is interesting to contemplate how structures, which seem so significant to us, may be merely an epiphenomenon of rules that have evolved for reasons unrelated to the nest structure. This is particularly the case with the stingless bees where brood cells may be built as a semi-comb or a comb. We humans attach great importance to this distinction (see above), but as we shall see, the difference likely arises as a consequence of how queens and workers interact during the cell provisioning and oviposition process (POP), and not as a direct effect of selection on comb architecture.

In the stingless bees, brood cell construction is intimately associated with the provisioning of the cells with food, egg laying, and cell capping (Sakagami, 1982; Zucchi et al., 1999). Ethologists recognize that the POP is part of 'an ancient struggle over egg laying and oophagy' (Hamilton, 1972) in which the queen monopolizes newly constructed cells, and either prevents workers from laying in them or eats the eggs if they do so. In some 'primitive' species, the POP is associated with overt aggression between workers and queen, and only one brood cell is constructed at a time. In other species, the aggression has been all but lost, and large numbers of cells are built simultaneously in different parts of the nest, and the construction of each cell is independent of the presence of the queen. This can only occur in species where worker egg laying is rare or absent. A quick tabulation suggests that comb construction only occurs in those

Table 2 Nest Characteristics of the *Trigona carbonaria* Species Complex of Australian Stingless Bees

	Species			
Nest Characteristics	***T. carbonaria***	***T. hockingsi***	***T. mellipes***	***T. davenporti***
Comb type	Spiral comb	Semi-comb	Cluster	Semi-comb
Entrance tube	Absent	Absent	Present	Absent
Entrance ornamentation	Extensive	Absent	Absent	Minimal

species where multiple cells are produced simultaneously, spirals are built when cells are constructed simultaneously on multiple fronts, and clusters are produced when cells are produced one at a time (Table 2). This suggests that a seemingly unrelated character—the degree of queen dominance—is of singular importance in determining nest architecture. It is important to use caution here, in that the conclusion suggested in Table 2 has not been corrected for the possible effects of phylogenetic inertia.

9. CONCLUSIONS

We have argued that the nest architecture of the eusocial bees is an extended phenotype of a colony (Dawkins, 1999) and is thus under natural selection. The way natural selection must act to change nest architecture is to change the rules that individual workers follow as they build cells. Small changes in the rules followed by individual workers can lead to radically different outcomes. By the same token, the behaviour of cell-building stingless bees may be under selection in ways unrelated to the structure of the nest, so that different nest structures emerge in closely related species, merely as an epiphenomenon.

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